

# RECENT ADVANCES AND FUTURE NEEDS IN THE STUDY OF COLLEMBOLA BIOLOGY AND SYSTEMATICS

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## ABSTRACT

*Some new results from studies of collembolan feeding, reproduction, behaviour and response to chemical pollution and mechanical habitat disturbance are presented. Morphological variation in terms of ecomorphosis, cyclomorphosis and epitoky is discussed. A future expansion into the fields of cytogenetics, physiology and functional morphology is expected to accelerate taxonomic refinement of current systematics.*

## RÉSUMÉ

*L'auteur présente des données nouvelles sur l'alimentation des Collemboles, leur reproduction, leur comportement et leur réaction à la pollution chimique et aux perturbations mécaniques de leur habitat. Il discute de variation morphologique en termes d'ecomorphose, de cyclomorphose et d'épitokie. L'expansion éventuelle dans les domaines de la cytogénétique, de la physiologie et de la morphologie fonctionnelle devrait accélérer le raffinement taxonomique de la systématique actuelle.*

## BIOLOGY

### Introduction

As one of the major groups of soil microarthropods, Collembola has received increasing attention from ecologists and biologists during the few last decades. Collembola biology has become a very complex and multifaceted field of research. It is impossible in just a few pages to outline all aspects of current Collembola biology studies. Instead, I will select a few important aspects of Collembola life such as feeding, reproduction, behaviour, reactions to chemical pollution and dependence on moisture - probably the one external factor that has the greatest effect on Collembolan life.

### Feeding and nutrition

Apart from a few predaceous species, most Collembola feed upon a variety of organic material, both detritus and living substances, such as algae, fungal hyphae and bacteria. A considerable amount of inorganic material may pass through the digestive tract as well. Some authors regard soil Collembola as rather generalized feeders (Anderson & Healey, 1972; Greenslade & Greenslade, 1983). Others are of the opinion that they are more or less selective (Hale 1967). In either event, certain food preferences - depending on species, habitat and time of the year - are frequently reported (McMillan 1975, Vegter 1983). The coexistence of 15-20 species of Collembola in a small volume of soil may indicate that either there is a surplus of food, or that the food is partitioned by subject or by microhabitat differentiation of the involved species. The latter is obviously possible. Even a few centimeters of a soil profile is rarely uniform from top to bottom, offering a variety of habitats. But it is more difficult to explain

how nine different species of surface active *Isotoma* could occur together in a handful of damp tundra soil in north Alaska, unless there is some kind of food specialization or an excess of food (Fjellberg, unpubl.)

The uniformity of the mouthparts in large groups of Collembola has been interpreted as an indication of unspecialized feeding (Greenlade & Greenlade, 1983). However, I think this is an oversimplification. Although built around the same model, the actual construction of individual parts of the feeding apparatus varies considerably, even in close systematic groups (Fjellberg, 1984a, 1984b). And what else other than food or feeding specialization could lie behind this quick adaptive evolution? Or, to put it another way: if two related species shared the same food, why should they differentiate their feeding apparatus? I believe we still have a very crude impression of how and on what individual Collembola species feed in natural habitats, and how they interact with other members of the community. It is a great challenge to students of functional morphology and to persons who want to develop techniques for studying Collembola feeding both in laboratory and in nature.

### Reproduction

As soon as the individual can keep itself alive by feeding, it must keep the species alive by reproduction. In understanding the reproductive biology of Collembola, we need information about life cycles, recruitment, mortality and other parameters. The size distribution of individuals in field populations - measured at various times during the year - has been used for a long time to obtain basic information about life cycles under natural conditions (Agrell, 1941; Fjellberg, 1975; Addison, 1981). A closer demographic analysis, involving some mathematical modelling, may also provide information about recruitment and mortality, which are essential factors in the energy budget of a population (Hale, 1980; Straalen, 1982, 1983). Data about fecundity, the potential number of eggs produced by a female, has accumulated from a number of laboratory studies. From these studies, individual fecundity appears to be rather flexible, influenced by population density (crowding), age of the individual, temperature, substrate, and other things (Hutson 1978, Snider 1973, Snider 1983). Concerning life cycles and longevity, it is clear that the long arctic winter arrests development and delays reproduction until individuals are 1-2 years old (Fjellberg 1975, Burn 1981, Addison 1977, 1981). Mature specimens may live for several (3-7) years and may reproduce several times. A winter diapause is demonstrated in several species, and is supposed to be essential for synchronization of the spring reproduction of adults in the European species *Hypogastrura socialis* (Uzel). This species has a rather fixed reproductive pattern. Adults reproduce only once in spring, and die shortly after. Pheromones appear to be essential for the group behaviour of this species (see later) (Leinaas, 1983b).

Collembola living in cold environments have clearly adopted an opportunistic reproductive strategy. Overwintering may occur in any stage of development and life cycles are adjusted to physical conditions of the habitat, which sometimes gives different life cycles in different cohorts of the population (Addison, 1977) or in different populations along a microclimatic gradient (Tamara & Mihara, 1977).

In temperate and warmer regions the generation time is shorter and reproduction runs more freely, giving a very complex age structure with indistinct cohorts (Petersen 1980, Tanaka 1970).

## Behaviour

The study of behaviour and behavioural ecology of Collembola will probably receive increased attention in the future. At first consideration, the behaviour of a springtail may seem odd and bizarre. However, with closer inspection, we usually find that the behaviour is very reasonable and part of the solution to fundamental biological or ecological problems. Bretfeld (1970, 1971, 1976a, 1976b) described the rather complex mating systems and sexual interference in different species of sminthurids. Although the Collembola do not have a direct copulation and sperm transfer, the mating behaviour is probably part of the isolating mechanisms between species, just as in other groups of arthropods.

The mass occurrence of Collembola - especially on snow - is frequently noted. Less often seen, but probably of greater significance, is the aggregated occurrence of Collembola in soil and litter, where they sometimes form dense colonies of millions of individuals. We have now gained some insight into the mechanisms regulating this particular behaviour. Verhoef *et al.* (1977) and Mertens & Bourgoigne (1977) reported aggregation pheromones in Collembola. Leinaas (1983b) found a strong dependence on pheromones and phototaxis in the activity of two species of *Hypogastrura*. Leinaas & Fjellberg (1984) found a strict sun orientation in migrating colonies of an alpine *Vertagopus* species in Norway.

The social behaviour, resulting in smaller or larger aggregates, is partly interpreted as an adaptation to patchy, ephemeral habitats (Leinaas, 1983b), or - to put it in other words - to the non-random distribution of food, optimal moisture conditions, breeding sites, overwintering sites, *etc.* Obviously, pheromones help to keep the colonies together in favourable spots, as well as to coordinate their movements when they have to leave the area.

Curious enough, the mass occurrence on snow often results from the disintegration of colonies living on ground in the snow-free period. Activity on the snow surface probably acts as a way of dispersal in species that feed and breed in island-like habitats such as tree trunks, compost heaps, *etc.* A number of these "snow-fleas" also have a special winter morph with modification that possibly makes movement on the snow easier (Leinaas, 1983a).

## Dependence on moisture

Moisture is probably one of the most important factors influencing the daily life of the Collembola. Unlike many other arthropods, Collembola have no hard exoskeleton that prevents evaporation from the body surface. Much research has been done on the water balance of Collembola, stressing the importance of keeping down the loss of water vapour from the body surface. Two different strategies seem to be followed. (1). Either the Collembola live in a constantly damp environment like deep soil or in caves, which makes special adaptations to dry air unnecessary. Some species of this group have completely lost their ability to control water loss (Vannier, 1977). (2). Some species have a variety of morphological adaptations to reduce the transpiration from the body surface, like scales and dense cover of hairs. This is combined in many species with an ability to actually survive shorter or longer periods with reduced water content of the body. In dry periods the species *Xenylla maritima* and *Vertagopus westerlundii* become visibly "shrunken", but are still active (Leinaas & Fjellberg, 1984). An extreme example is the inactive but reversible anhydrobiotic stage reported from several species in the Mediterranean region (Poinot, 1968, 1974). This anhydrobiosis is also combined with the ability to survive extreme cold, as much as  $-180^{\circ}$  below zero (Poinot-Balaguer & Barra, 1983). But so far no arctic species has been demonstrated to switch to this mode of surviving the winter.

Some species have behavioural adaptations, regulating their activity to times with high substrate moisture (Leinaas & Fjellberg, 1984). Certain xerophilic species react the other way, seeking drier places when substrate becomes too damp (Vegter, 1983; Bauer, 1979).

### Effects of pollution and human activities

Increased attention is paid to the ability of Collembola to live in a polluted environment. Detoxification mechanisms are found in several soil dwelling groups, like molluscs and earthworms. In Collembola certain poisonous metals are accumulated in midgut cells and leave the organism during moulting when the midgut cells are also shed (Humbert, 1974, 1977; Joosse & Bucker, 1979). Thus, the Collembola may cope with fairly high levels of metals without any immediate lethal effect. However, Joosse & Verhoef (1983) found reduced metabolic rate and lowered reproduction in Collembola which were experimentally fed on lead-contaminated food. Also Bengtsson *et al.* (1983) found reduced growth rate in the euedaphic *Onychiurus armatus* fed on Pb+Cu contaminated fungi, giving an equilibrium concentration of about 200 ppm copper in live specimens. Similar concentrations were found in a natural population of *O. armatus* in the vicinity of a brass mill. Copper is essential in respiration enzymes, and moderate levels actually increased growth rate of *O. armatus*.

A similar fertilizer effect was reported by Hågvar & Kjøndal (1981) who found an increase in density of some species in litter bags treated by simulated acid precipitation. The authors indicate a better reproductive success in "acidophile" species in litter bags with lowered pH as a possible reason for this increase.

Chemical pollution, directly affecting the physiological processes of the individual, is certainly different from the more technical disturbance of the habitat caused by activities like logging, grazing and plowing. Certain opportunistic species clearly benefit from man's activities. Greenslade & Greenslade (1983) found an increase of *r*-selected opportunistic isotomids in disturbed soils in the Solomon Islands. Unfortunately, such a faunal shift has a negative effect on the more special *K*-selected species. And these species are often stenotopic, rare and need special protection. Work in progress indicates a serious impoverishment of the endemic Collembola fauna of Hawaii (Bellinger, pers. comm.). If it is correct that arctic Collembola in general are opportunistic, as Greenslade (1983) puts it, it shall be interesting to see if they will be better off in man-made and altered habitats than their tropical relatives.

Collembolan species and assemblages have become subjects for testing ecological theories that were originally developed on vertebrates and better known groups of arthropods. I have already mentioned MacArthur & Wilson's (1967) continuum of *r*- and *K*-selection, which has now got a third dimension, the adversity or *A*-selection of Greenslade (1983) who partly used Collembola to develop the hypothesis. In future, Collembola will certainly receive increased attention from students of fundamental ecological and evolutionary processes. Such studies will probably detect and illuminate a number of taxonomic problems. And this brings me to the second part of this presentation, the systematics.

## SYSTEMATICS

### Introduction

The majority of collembolan taxonomists have worked in European countries. The various European schools have developed new analytical approaches to understanding structure and classification of Collembola. Consequently, the European fauna is fairly well known.

In North America, Collembola has been a much neglected group, probably because so few of them are pests in agriculture and forestry. The precise identification of North American species has been difficult due to lack of required literature. The recent, monumental work of Christiansen & Bellinger (1980, 1981) has altered this situation. However, their work is a preliminary and partly synoptic presentation of the fauna, serving as a platform for the future monographic work which is necessary. A few small soil samples from almost any part of North America will produce one or more undescribed species. Thus the North American fauna is a great challenge to taxonomists and a tremendous source of primary material for studies in classification, evolution and phylogeny. In the following paragraphs I describe some of the biological phenomena underlying the frequently observed intraspecific variation in morphology.

### Ecomorphosis

The Collembola have direct development with continued growth throughout life. The various instars are separated by ecdysis in which the old cuticle is shed. Apart from the small changes related to increased size, development of hair cover and reproductive organs, more drastic changes may appear as a response to both intrinsic and external stimuli.

In a number of papers Cassagnau (1955, 1956, 1971, 1974) described ecomorphosis both in Hypogastruridae and Isotomidae. Ecomorphic specimens had enlarged setae and cuticular ridges and spines on the last abdominal segments. Also mouth parts, digestive tract and fat reservoirs of the body were affected. Ecomorphosis was supposed to be a physiological response to warm and dry conditions in species having their optimum in damp, cool, habitats. However, recent studies by Najt (1982) give a more complex interpretation. Given enough time, the classical species *Isotoma tigrina* (*olivacea* auct.) would produce ecomorphic specimens even at 5° C. Sooner or later all individuals would pass through one or more ecomorphic instars. Contrary to earlier reports, Najt also found that some of the ecomorphic specimens had normal digestive tracts and would feed. Apparently the onset of ecomorphosis is genetically fixed in the species and not a simple response to unfavourable microclimate.

Najt's observations open some very interesting perspectives. A number of isotomid genera always have abdominal spines and cuticular modifications which are essentially the same as in ecomorphic species displaying these structures in certain instars only. It seems possible that there is an evolutionary sequence from normal, "non-ecomorphic" forms to forms displaying ecomorphic traits in certain instars only (induced or not induced by external factors), to forms in which ecomorphic traits have become permanently fixed in all instars (all the "spined" isotomid genera, *Anurophorus*, *Proctostephanus*, etc.). Modifications of the digestive tract are no longer associated with this last stage, but individuals still benefit from the reduced evapotranspiration (modified cuticle) and may occupy rather xeric habitats.

### Epitoky

Another phenomenon giving similar anatomical modifications as ecomorphosis, is epitoky. Epitoky is linked to the reproductive cycle and is only shown by reproductive specimens. It is quite common in many genera and affects various parts of the body, generally with reduction or modification of anal spines, claws, dens and mucro, body setae and skin granules (Bourgeois, 1971, 1973, 1974, 1981). Males of some *Vertagopus* get enlarged antennae (Fjellberg 1982).

### Cyclomorphosis

A third phenomenon affecting the individual during its life cycle, is cyclomorphosis - the occurrence of seasonal forms not linked to the reproductive cycle or ecomorphosis (Fjellberg, 1976). Usually this involves the appearance of distinct summer and winter forms. Sometimes a switch from the one form to the other is associated with a shift in habitat. Certain *Hypogastrura* species have summer forms living on tree trunks while the winter forms are active on snow. The morphological changes are supposed to facilitate movement on the snow surface, and thus aid in the dispersal of the species (Leinaas, 1983a). Of particular interest are the clavate tibiotarsal hairs that appear in the European *Isotoma nivea* Schäffer during winter. Following traditional systematics, the winter form would be classified as a *Vertagopus* (Fjellberg, 1978).

Studies of the above phenomena are in an early stage. We know very little about the evolutionary significance and what it means to the individual. A number of examples are still to be detected and described. Among North American *Hypogastrura* of the *nivicola-packardinotha* groups, there are a number of forms displaying cyclomorphosis. Some of the currently recognized species are probably just seasonal forms of each other.

### Chaetotaxy

In former days Collembola systematics was based on easily visible characters like number of eyes, presence/absence of certain organs, fusion of body segments, claw structures, position and shape of sensorial organs, etc. Such characters still rank among the most important, but must be used with caution as several of them are affected by the phenomena described above.

During the last two decades, several new analytical methods have come into use. One of the most promising is probably the strict use of chaetotaxy, the mapping of the body hairs. In the more primitive families of Collembola the hair cover is fairly simple and each seta has a more or less fixed position. In more advanced groups, hair cover is dense and irregular, and chaetotaxy is applied to certain parts of the body like furca, mouth region and antennae, or to "markers" like body macrochaetae or sensillae.

Chaetotaxy often provides clearcut differences among related species. Apparently evolution of the hair cover is a fairly rapid process with a high degree of parallelism even in species groups within a single genus (Fjellberg, 1984c). A general trend seems to be reduction in number and dislocation and differentiation of setae (Bourgeois & Cassagnau, 1972). Chaetotaxy as a method has developed in a rather individualistic way. Different specialists have produced more or less independent systems (Gama, 1969; Rusek, 1971; Cassagnau, 1980). An important aim for future research would be to develop a common system, making possible a comparison between distant taxa.

### Cytogenetics and physiology

During the last few years, biochemical methods, cytogenetics and physiology have come into use to discriminate between species. Hale & Rowland (1977) used protein electrophoresis and amino acid chromatography and found convincing differences among forms of the problematic *Onychiurus armatus* group. Hart & Allmong (1979) made an electrophoretic analysis of esterase enzymes in species from various genera and found consistent differences. These biochemical methods are promising and may also trace populational characteristics which are not detected by traditional studies. Dalens (1982) found differences in amino acid composition in two populations of *Hypogastrura tullbergi* (Schäffer). Such differences were also

documented by studies of polytene chromosomes in *Bilobella aurantiaca* Caroli by Cassagnau (1976), Dalens (1976, 1977, 1978, 1979) and Dallai (1979). The giant chromosomes display a varying degree of polymorphism, and offer a great potential for mapping populations of different origin (Cassagnau *et al.*, 1979; Deharveng, 1982a). Even the existence of sibling species is indicated by some authors (Dallai *et al.*, 1983). Although chromosomal studies are limited to a small section of the family Neanuridae, they provide valuable information to clarify species concepts and to understand population genetics of Collembola in general.

### Future approach

Sitting by the microscope to observe and make drawings is still the same approach that was used by the pioneers in Collembola systematics a hundred years ago. Although we have better quality microscopes and benefit from all the accumulated experience, the species identification of a collembolan is technically much the same as in "good old days". When the scanning electron microscope (SEM) was introduced some years ago, many people expected a revolution in the morphological studies of small organisms - of course with certain consequences to established classifications. I think it is correct to say that this has not happened in Collembola. Certainly the SEM has revealed some interesting developmental lines in surface structure of the cuticle as well as the fine structure and possible function of some sense organs. But, in routine identification and in ordinary work, the light microscope is superior.

Progress in Collembola systematics will probably not come as a result of new technical inventions - although much might happen in the fields of biochemistry and cytogenetics. There are still some parts of the collembolan body which have not - or only rarely - been used in practical identification and systematic work. The mouth region is one of the most promising. Apart from the often very complex maxillae and the simple mandibles lying inside the head, there are the external maxillary lobes, the labium, labrum and associated structures. The internal mouthparts, especially the maxilla, are commonly used in the families Neanuridae and Isotomidae, partly also Hypogastruridae (Massoud, 1967; Poinso, 1965; Fjellberg, 1977, 1984a). The labium has proved very significant in Entomobryidae and other families (Gisin, 1965; Christiansen & Bellinger, 1980; Deharveng, 1981). In a recent paper I drew attention to the maxillary outer lobe which is particularly useful in species separation in the bulky genus *Isotoma* (Fjellberg, 1984b).

As I have argued earlier I think the differentiation of the mouthparts reflects a progressive food specialization, and I believe that combined studies of structure, function and actual type of food ingested might produce some very interesting results.

In order to have success today, a taxonomist has to construct a phylogenetic tree - a cladogram. The necessary tools and methods are only partly developed in Collembola. Chaetotaxy has been used by a number of workers (Gama, 1969, 1980; Najt, 1974; Deharveng, 1982b) as well as distribution of body tubercles in Neanuridae (Cassagnau, 1983; Deharveng, 1982c). Reduction seems to be a universal principle in Collembola. Number of hairs are reduced, ocelli are lost, furca becomes shorter and finally disappears. However, several structures increase in complexity, like the feeding apparatus, the claws, the differentiation and shape of individual body hairs, and so on.

There is still a lot of work to be done before the relative plesimorphy/apomorphy of the various character states along a transformation series can be established. In order to achieve reasonably sound conclusions, it is necessary to include as many species or samples as possible from the entire geographical area covered by the taxon under study. In this context, the rich

Nearctic fauna is particularly important as a pool of still unknown or inadequately described species.

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